Seasonal Polyphenism in *Artogeia napi* L. (Lep.: Pieridae)

By S. R. Bowden*

Just as the two sexes of a species have sometimes in error been given different "specific" names, so also seasonal forms of *Artogeia* subspecies have on occasion been named independently by the same or by different authors. The younger name should then fall as a synonym, but has often been retained as a name for the generation described; excessively fertile authors have even invented names deliberately to give every subspecies two or even three seasonal designations. How a "spring" form caught in high summer is then to be treated I am uncertain. Names such as *aestivoautumnalis* Müller do, however, raise *some* interesting questions.

Normal Seasonal Dimorphism

In general, marked seasonal dimorphism in bivoltine Holarctic butterflies is limited to those species in which some pupae undergo a winter diapause and some do not. Thus *Celastrina argiolus* L. shows distinct forms, whereas the two emergences of *Lysandra bellargus* Rottemburg are indistinguishable.

At the turn of the century, when Merrifield (1893) and Weismann (1896) were writing, the seasonal forms were thought to be generated by temperature differences at some stage of development. Later, day-length was implicated, and as recently as 1970 Oliver stated of *A.* (*napi*) *oleracea* Harris: "It is impossible yet to say whether it is the larval photoperiod itself or the occurrence of diapause in the pupa that actually directly determines which phenotype is to be produced, since larval photoperiod and diapause cannot here be separated".

However, Thompson (1947) alludes to "the simple and inescapable truth of the matter, which was explained by Jarvis (1942). There are two forms only; that in which development is arrested in the pupa throughout the winter, and that in which development continues without definite halt . . . until the emergence of the imago". Thompson reached this conclusion after rearing 150 broods of British *napi.* I can confirm its usual validity after thirty years' breeding of material from about twenty European, American and Asiatic populations — and from their hybrids. But I think the behaviour of *A. napi* is not always predictable.

The general situation is well put by Oliver (1970) and further experimental evidence is hardly required to establish the direct connection of the seasonal forms with the diapause/non-diapause alternative. The seasonal phenotypes that Oliver illustrates are those of the undersides of ssp. *oleracea,* a subspecies particularly suitable for his purpose, since the "spring" form carries dense, sharply defined black veining, whereas in the "summer" form the narrow veining is nearly unpigmented. *Artogeia napi napi* seasonal undersides are less contrasted, but this subspecies shows well-known differences

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on the upperside. Nevertheless Oliver's conjecture that *oleracea* and the European insect may have different systems of regulating seasonal development is unduly cautious. His uncertainty whether phenotype is determined directly by photoperiod or through photoperiodic induction of diapause is perhaps resolved by examination of those broods, reared uniformly at the same temperatures and photoperiods, in which part of the larvae produce non-diapause pupae (so-called "S" pupae) while the remainder ("L" pupae) lie over the winter. The S pupae yield the summer form, the L pupae the spring form. Such split broods occur very commonly, even usually, in British *napi*; most other subspecies, including those univoltine in nature, can become partly multivoltine in particular circumstances. Shapiro (1975) has recently established this for *A.* (*n.*) *microstriata* Comstock; breeders of the European *A.* (*n.*) *bryoniae* Ochsenheimer and *A.* (*n.*) *adalwinda* Fruhstorfer and of the American *A. virginiensis* Edwards will have met with occasional S emergences from their cultures — the phenotypes depart from the usual ones just as S forms normally differ from L forms.

The pre-pupa undergoes the S or L pattern of development according to the photoperiod in which the larva has been subjected, but this control does not operate uniformly. For practical purposes it is often convenient to induce L development by subjecting the larvae (after the first instar) to 16-hour nights. This is nearly always effective for pure subspecies. S development on the other hand is encouraged by long days, but is not ensured, since a genetic bias towards diapause (not always suspected in advance) may negative the response to photoperiod.

Irregular Diapause

So far we have assumed that all non-S pupae will lie over the winter, not even completing diapause till perhaps some time in January — after which warmth can induce imaginal development. It is usually safe to say that if there is no visible development in 14 days at ca. 20°C. the pupa is in normal diapause. But in some hybrids one sex may enter a "weak" diapause only, and eclose at some quite incalculable time. Less frequently this may happen in pure subspecies, irrespective of sex. I have reported (1966) the case of an apparently uniform batch of wild Corsican *Pieris brassicae* L., of which 10 females and 7 males eclosed 8-10th June, a further male on 2nd July, two males on or just before 12th August, and one male on 9th October, leaving none to over-winter.

During the past year (1977) alone there have been three comparable examples:

(1) On 25th October I received from Dr. F. Chew ca. 100 pupae of *A.* (*napi*) *oleracea,* formed by wild-collected Vermont larvae. Pupation had been before 25th July in every case, and there had been no subsequent refrigeration. On 8th November a female eclosed, of modified summer form, i.e. very narrow hindwing underside veining with light melanin pigmentation.

(2) Between 8th and 14th June, 26 adults of *A. melete melete* Ménétriès (brood 1977-*H*), reared from Tokyo eggs kindly given by Mr. T. Takakura, eclosed. On 1st October a cursory examination of the remaining 11 pupae (all of which had been reared separately with 16-hour nights and should have been in diapause) showed that a female adult had emerged and was still alive. Another of the pupae produced a female on 3rd October, after which the remainder were refrigerated. The phenotype of the last female, after its summer diapause of 3½ months, was of "spring" aspect (though not extreme), having well pigmented veining.

(3) A large hybrid brood 1977-*k* was obtained from a mid-June pairing of a Davos Platz *A.* (*napi*) *byroniae* female with *A. melete* ♂ *H7*. Emergences of 70 females, 6 males and one sex-mosaic took place in August. Two further males eclosed in the latter half of September. Emergences then seemed to be complete, and thereafter the boxes containing the pupae were "lost" till mid-October, when it was found that 9 more males had emerged, most of them being already dead. A large final male eclosed on 17th October, and 52 pupae were placed in refrigeration.

This last brood exemplified the sexually biased disturbance of diapause-control by hybridisation (Bowden, 1953, 1955). After 24th August, 12 males only came out, whereas the previous 6 had accompanied ten times as many females. The last male had a "diapause" of around two months only; its phenotype is probably best considered intermediate.

Intermediate and Extreme Phenotypes

What phenotype is to be expected in short-diapause butterflies? Does a distinct "*autumnalis*" form occur? Here it is necessary to consider how much, if any, environmental (temperature) variation occurs in S individuals. There is, of course, a good deal of confusing genetically determined variation.

It should be made clear that in L pupae a high temperature does not break diapause. Indeed, as is well known, pupae taken out of refrigerated storage too early in the winter and forced at 25-30°C. ultimately die without eclosion unless returned to the cold for a further period.

Though basically correct enough, Thompson's (1947) statement has to be qualified. If one takes a subspecies with very different seasonal forms, such as *meridionalis* Heyne of Corsica or *oleracea* of New Hampshire one finds that the extreme summer form with much-reduced underside veining characterises the emergence of high summer, but that autumnal emergences (often partial only), though still close to summer form, tend to depart from it slightly in the direction of the diapause generation. To that extent an autumn form does exist, but it is not distinct. In another subspecies with less marked seasonal difference, such as the English *septentrionalis* Verity, a specimen may on rare occasions be difficult to allot correctly as a diapause or a non-diapause individual. But whereas a chilled S pupa may produce an intermediate, heating a dormant L pupa which has completed diapause does not seem materially to alter the spring phenotype.

In July 1970, an experimental batch of 33 refrigerated pupae of wild Hertfordshire stock was divided: after two days at room temperature, 17 were placed in an incubator at 26°C., 16 in a wet-fabric cooler at ca. 13-16°C. Emergences took place after a further 6-7 and 17-19 days, with one death in each lot. The adults were set as undersides in two rows, males opposite males and females opposite females. The rapidly developed insects were then obviously a little more extensively dark-veined than the others, with minimum overlap between the series — so that here heat even intensified the L pattern. Nevertheless, none departed significantly from the "spring" type.

There is, however, an artificial "super-spring" form which is produced, apparently, by holding over-wintered pupae (which have completed diapause) for some months at varying temperatures between 0°C. and about 6°C. Some individuals, though not all, then develop phenotypes with exaggerated "spring" characters, i.e. discal spot markings disappear completely or almost completely in both sexes, even on the underside, and the radial veins on the upperside are more or less blackened throughout their length. The result may be a fair phenocopy of the almost unmarked "restricta" upperside which characterises ssp. *oleracea* and *virginiensis* (but not *venosa* Scudder) in America.

Regrettably it is not yet possible to specify precisely the conditions which yield the "super-spring" form. It has appeared frequently but sporadically as a consequence of temporary refrigeration inadequacies, the primary effect of which on temperature variation has not been monitored. Moreover, individuals seem to differ in their liability to respond in the manner described, though many subspecies are susceptible.

The exact stage of post-diapause differentiation which is sensitive to slow or intermittent development may be difficult to decide. One can conjecture that it is interruption or continuity at nearly the same critical stage that determines the usual L or S phenotypes. Shapiro (1977) hopes to detect the initial reactivation of diapause pupae by monitoring their respiration (references given by Tauber, 1976), and to apply alternative temperature regimes at this point. The existence of the "super-spring" form does seem to make the pre-diapause initiation of the seasonal phenotype less likely. Also, once the pupal stage is reached, photoperiod is probably irrelevant in *Artogeia*.

Conclusions

As the breeding of certain hybrids also confirms, melanic markings on the wings of *Artogeia* comprise several genetically determined pattern-systems which appear to be activated or inactivated separately and probably have different temperature coefficients. Pupae monitored as having just completed in-diapause changes are required for experimental investigation of thermal effects on post-diapause pattern development.

In *Artogeia napi*, exceptionally, phenotypes other than the "spring" and "summer" forms normal for the subspecies concerned may be produced. Late summer ("autumn") forms are generally summer forms modified to a variable extent. The artificial "super-spring" phenotype mimics the "restricta" form developed even in European stocks when they are made homozygous for a recessive gene present in ssp. *oleracea*.

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February in Hampshire. — The temperature on the 11th at 11.30 p.m. was 27°F. By the 16th snow lay from 4 in. deep and temperatures were still at freezing point. From the 16th to 22nd snow drifts up to 6 ft. deep blocked many roads. On the 23rd it was warm and most of the snow had thawed. The temperature on the 24th at 11.30 p.m. was 50°F. and I recorded the following at my m.v. light: *Phigalia pilosaria* D. & S. (Pale Brindled Beauty) (21), a record for one night; *Erannis leucophaearia* D. & S. (Spring Usher) (6), not recorded before from the garden; *Theria rupicapraria* D. & S. (Early Moth) (5), a record for one night; *Operophtera brumata* L. (Winter Moth) (1), not previously recorded in February in my garden; *Conistra vaccinii* L. (Chestnut). After this remarkable night, one wonders what the rest of 1978 will hold. — R. A. Bell, Northwood Lodge, Northwood Park, Sparsholt, near Winchester, Hants.